PLEISTOCENE BIOGEOGRAPHY OF TEMPERATE DECIDUOUS FORESTS

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ABSTRACT

Recent evidence on the number and timing of glacial-interglacial cycles during the Quaternary will influence ideas on the biogeography of plant communities. Each cycle includes 50,000 to 100,000 years in the glacial phase and only 10,000 to 20,000 years in the interglacial phase.

During glacial phases deciduous forests were eliminated from Europe north of the Alps; the sequence of immigration during each interglacial was different, and consequently there were different communities of forest trees. Each interglacial cycle shows progressive leaching and acidification of soils, which caused further changes in the abundances of trees.

In America the interglacials are poorly known, but the Holocene serves as an analogy for previous cycles. The warmest (and driest, in some areas) part of the interval was 5000 to 8000 years ago. Forest trees migrated to their present ranges from different source areas—hickory from the west, chestnut from the east. Those that reached their northernmost limit during the warmest part of the Holocene, such as beech and hemlock, have been decreasing in abundance in the last few millenia; others still show expanding populations as their ranges continue to extend westward or northward (hemlock, white pine, and beech at their western limits; perhaps chestnut prior to the blight at its northeastern limit). The role of progressive soil development in influencing these changes has not yet been investigated.

Although the present interglacial interval is nearly over, the flora of northern United States is far from equilibrium. Since all previous interglacials were of similar length, one can generalize this result to all previous interglacials. Modern species evolved during an epoch characterized by climatic and floristic instability; presumably they are adapted for successful penetration of closed communities in order to survive the rapid environmental changes that have characterized the Pleistocene.

INTRODUCTION

Recent developments in geology change profoundly the traditional views of the effect of Pleistocene glaciation on plant distributions. These developments include the discovery of multiple, relatively brief, glacial cycles—perhaps as many as sixteen during the Pleistocene alone (Hays *et al.*, 1969). Absolute chronologies establish the base of the Pleistocene at 2 million years, providing a time span averaging only 125,000 years for each complete glacial-interglacial cycle.

A second important development concerns the relative durations of glacial and interglacial phases. Traditionally geologists and biogeographers have thought that the phases were of subequal lengths, assigning the greater time span to the interglacial phase. The present interglacial configuration of vege-

GEOSCIENCE AND MAN, VOLUME XIII, MARCH 15, 1976, P. 13–26, 11 FIGURES

tation has been considered normal for the Pleistocene, with plants and animals pushed southward to survive in warm "refugia" during brief glacial episodes (MacArthur, 1972; Flint, 1957). New extrapolations from the thickness of sediment in dated ocean cores (Emiliani, 1972; Hays and Perruzza, 1972), from the numbers of varves in lake deposits (Wright, 1972), from uranium series dates on marine terraces (Broecker *et al.*, 1968), and from the numbers of pollen grains incorporated into interglacial sediments (Dabrowski, 1971) are in agreement that interglacials (the part of the cycle with temperatures equal to or higher than today's) lasted only 10,000 to 20,000 years. In contrast, each glacial phase lasted for 50,000 to 100,000 years (Emiliani, 1972; Kukla *et al.*, 1972). During the glacial phases, there were major oscillations in temperature, but there was generally a cooling trend that culminated in maximum glacial extension toward the end of the interval (Broecker and Van Donk, 1970). These trends are apparent in Emiliani's (1966) generalized palaeotemperature curve for the last few glacial cycles, based on oxygen isotope measurements from ocean cores (Fig. 1). The dashed line drawn at today's oxygen isotope levels in Figure 1 shows that few levels exceed this —only 10% of the total, while 90% indicate water temperatures colder (or ice volumes greater [Dansgaard and Tauber, 1969]) than those of today (Emiliani, 1972). Two important generalizations emerge from this fact: 1. The present warm climate interval, the Holocene, is entirely analogous to previous interglacials. It began 10,000 years ago and reached a temperature maximum 5000 to 8000 years ago. The present thus represents conditions similar to those near the end of a normal interglacial interval (Kukla *et al.*, 1972; Wright, 1972). 2. The configurations of climate, flora, and fauna during the glacial periods have been the predominant configurations during the last 2 million years. Therefore glaciation, in varying degrees greater than today, must be considered the normal phase, having prevailed during the time of the evolution of modern plant and animal species. The Pleistocene must be viewed as a cold, glaciated epoch, interrupted periodically by catastrophic warm events —the brief interglacials with climate similar to that of today.

Plant migration does not occur instantaneously, but at a finite rate that depends not only on the dispersal characteristics of a particular species, but also, and probably more importantly, on the changing physical and biotic environment. Migration rates are measurable; the record of the present interglacial and previous interglacials shows that floristic equilibrium is never attained, at least at high latitudes, before glacial conditions set in again. In this sense, the interglacials are unstable interruptions in Pleistocene history. Soils also show continuous development throughout interglacial periods, indicating that interglacials are too short for attainment of an ecosystem equilibrium.

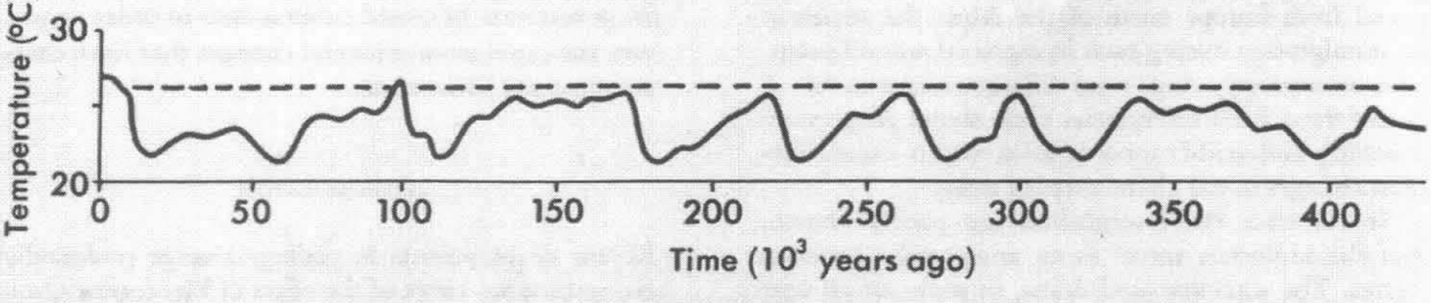

FIGURE 1. Generalized temperature curve for surface waters of the Caribbean, based on oxygen isotope ratios in fossil planktonic foraminifera recovered from ocean cores (from Emiliani, 1966). A dashed line has been drawn across the graph at the isotope ratio achieved 10,000 years ago, after the beginning of the Holocene. Note that few parts of the curve approach or exceed this value, indicating that glacial climates have characterized most of Pleistocene time, while interglacials as warm as the Holocene have been rare events.

THE GLACIAL PHASE OF THE GLACIAL-INTERGLACIAL CYCLE

Any consideration of Pleistocene biogeography must emphasize the distribution of flora and fauna during glacial phases. Until recently almost nothing was known in North America, and although extensive studies were available for north of the Alps in Europe, relatively little work had been done in the Mediterranean and Middle East. Biogeographers tended to view the southern Appalachians and the Mediterranean region during ice ages as lush refugia for the temperate flora and fauna. Therefore it has come as a surprise to find that both regions were characterized by a cold, dry climate during the glacial maximum. Temperate mesic species, now so widespread and familiar to ecologists, must have endured much of the Pleistocene epoch as rare and endangered species, in small areas of favorable climate. Most of these areas have not been identified with certainty.

The deciduous forests that had prevailed throughout Europe during the climatic optimum of the last interglacial changed toward the end of the interglacial, with boreal elements becoming more abundant. Then a sharp lowering of temperature occurred about 100,000 years ago. Suddenly in northern Europe (Netherlands, Denmark), the boreal forest was replaced by more open vegetation (van der Hammen *et al.*, 1971). A number of climatic oscillations followed, with tundra or park-tundra in each cold phase and boreal forest returning during the warmer phases. As time went on, temperatures dropped and forests disappeared. Virtually all of Europe north of the Alps supported tundra vegetation only. Long intervals of time between 50,000 and 60,000 thousand years ago, and during the latter part of the glacial interval 15,000 to 25,000 years ago, were so cold and dry that polar deserts with little or no vegetation covered large areas. Frost action was intense, and ground was perennially frozen (van der Hammen *et al.*, 1971; Iversen, 1973).

Very recent discoveries of Pleistocene sediments in the Mediterranean region reveal that the landscape there was also largely unforested, with cold-steppe vegetation similar to that of modern steppe in central Asia. During warm and relatively moist intervals in the early part of the glacial interval, forests expanded periodically, incorporating deciduous trees and pine. In Macedonia, the forests disappeared entirely 60,000 years ago; the landscape was steppe until forests returned at the end of the glacial interval, 14,000 years ago. At higher elevations in the Balkans, there may have been a narrow forest belt where there could have been sites suitable for the survival of temperate deciduous trees (van der Hammen *et al.*, 1971).

New records of glacial vegetation in the United States reveal a surprising distribution of species. The early part of the glacial interval is poorly known, but a site in southern Illinois indicates prairie prior to 30,000 years ago (E. Grüger, 1972a, b). Open, xeric woodland with oak and pine grew at this time in the piedmont of Georgia (Watts, 1973a). During a warm interstadial interval between 22,000 and 28,000 years ago, spruce grew in the southern Great Lakes region, and boreal forests, with spruce and pine, near present-day Peoria, Illinois. Farther south, fossil pollen sites near Vandalia, Illinois, indicate mixed forests, with pine, birch, alder, and spruce. In Georgia, the warm interval caused oak and hickory forests to replace the xeric oak and pine woodland. Swamp cypress was present also. This species no longer occurs so far north of the coastal plain; the plant community was different from any known today. The evidence from Georgia and Illinois suggests that the early part of the glacial phase was characterized by dryness, with prairie or xeric woodland the prevailing vegetation. Unfortunately, we still do not know what the vegetation was like in other regions.

More dramatic changes in species distribution took place as the glaciation reached its culmination 20,000 years ago. The ice sheet was bordered by tundra—a narrow belt in Minnesota and Wisconsin, widening to more than 100 km in central New York State and Pennsylvania, and extending hundreds of kilometers farther south at high elevations in the Appalachian Mountains (Maxwell and Davis, 1972). The central plains were forest covered, and pine extended onto the plains from the Rocky Mountains (Hafsten, 1964; Watts and Wright, 1966); spruce grew in pure stands (with no pine) in Kansas, north to Iowa and east to central Illinois. In southern Illinois, spruce grew in mixed stands—apparently, prairie vegetation and forests with oak grew nearby. Along the Atlantic coast, in Virginia, there were mixed forests of spruce and pine, while to the south in the Carolinas and Georgia, jack pine (*Pinus banksiana*) grew in extensive stands, along with some spruce (Watts, 1970; Whitehead, 1973). Modern species distributions are a much greater geographical distance from glacial distributions than previously supposed (Deevey, 1949; Martin, 1958). For example, jack pine no longer grows within 1200 km of the sites in Georgia—its southern limit is now in central Michigan. Even more important is the disparity in community composition. The forests just described are different from the modern boreal forest, which is dominated by spruce and fir in eastern Canada, and by spruce and jack pine in central Canada. The full-glacial forest communities persisted at least 5000 years in some regions (Watts, 1970), changing little in Georgia between 24,000 and 13,000 years ago. These communities were stable (in the sense of not changing) longer than were communities in any temperate or boreal region during the Holocene.

The climatic change that marks the end of the glacial phase was sudden and of great magnitude. Rapid retreat of glaciers, especially montane glaciers (Denton, 1974), a sharp change in the oxygen isotope ratio in the Greenland ice sheet (Dansgaard and Tauber, 1969), and dramatic changes in fauna and oxygen isotope ratios in deep-sea cores (Fig. 1) combine to show that temperatures rose rapidly, changing 5° to 8° C between 15,000 and 10,000 years ago (Imbrie, Kipp, and Broecker, 1970). Continental glaciers, although slow to respond because of their great mass, began a rapid retreat at this time. In North America, ice margins in central Illinois and Long Island 18,000 years ago had retreated to the Lake Superior basin and beyond the north shore of the St. Lawrence river valley 10,000 years ago.

The response of vegetation and its movement northward into these newly deglaciated areas is the subject of this essay.

INTERGLACIAL VEGETATION CYCLES: EUROPE

The rapid rise in temperature 10,000 years ago in Europe created an unstable and rapidly changing vegetation. Many species were unable to migrate rapidly enough to keep up with the changing climates; unusual biotic communities developed, persisting only until invaded by competitively superior species. An example is the early postglacial vegetation in Denmark (Iversen, 1960). The climate was warm, as indicated by water plants now confined to temperate regions, but trees were absent from the vegetation for about 500 years. Juniper, already present although not flowering in the cold climate of the late-glacial period, expanded briefly, to be soon succeeded as a dominant by poplar. In this semiopen but lush community, large herbivores, such as the bison and Irish elk, were able to find forage. The diverse mammalian fauna from Late-glacial time was thus able to persist, with the exception of such species as reindeer, which are sensitive to temperature. However, as pine invaded the community and came to dominate it, producing shade and reducing grassy undergrowth, many species of herbs and large grazing herbivores were eliminated. The diversity of the vegetation decreased, but, unfortunately, the change is difficult to measure because plant species vary in their ability to leave a pollen record in sediments. Certainly the diversity of the mammalian fauna decreased.

Migrations of forest tree species and invasions of forest communities by new species continued in Europe throughout the Holocene, and up to the present. Beech is a striking example. This genus is rare throughout the Pleistocene sequence of western Europe (Godwin, 1956). It appears in abundance for the first time as fossil pollen 6000 years ago in southern Germany. The tree moved northward across Germany at a rapid rate, about 175 to 250 m per year (Firbas, 1949), and became dominant everywhere. It reached Denmark 3000 years ago, Great Britain 2500 years ago, and southern Sweden 1500 years ago (Berglund, 1966), In Denmark, the invading beech competed with linden (*Tilia*); pollen diagrams show that linden was replaced as a dominant by beech. Detailed studies implicate fire or grazing in the destruction of linden forests, indicating that invasion, or at least attainment of dominance in the forest, by beech was facilitated by human disturbance (Andersen, 1973).

Spruce was also a latecomer to European forests, moving westward and southward across the Scandinavian peninsula. Its rate of migration was most rapid in the north, apparently because it had little difficulty competing with pine and birch in the boreal forest. A slower rate of movement into the deciduous forests of southern Sweden can be calculated from pollen diagrams (Moe, 1970). The tree is now considered a desirable timber species, and it is planted extensively beyond its migratory frontier in southern Sweden. Beech forests in Scania beyond the limit of spruce have seedling spruce in the understory; the spruce are shade tolerant and will eventually become dominant in the canopy. Over time, the spruce needles that fall to the forest floor change the soil in a manner detrimental to beech. Of course the beech itself, although dominant at the moment, is a relative newcomer, having grown in that region for only 1500 years (Berglund, 1966).

Delayed spruce immigration is characteristic of all the previous interglacials. During the first interglacials, spruce was present but rare throughout, expanding late in the interval. In the last two interglacials and in the Holocene, spruce became extinct during the glacial phase, immigrating into Europe from its refuge area in the east long after the interglacial had begun (West, 1970). Andersen (1964) feels that the expansion of spruce and other species that characteristically grow on acid soils was predicated by progressive leaching. Nevertheless, once the soil was conducive to the growth of spruce, enabling it to compete successfully with deciduous forest trees, propagules had to move into northwestern Europe from source areas to the east. Hornbeam (*Carpinus*) is also a late arrival in most interglacial intervals. In Great Britain, the genus is rare in the Cromerian and Hoxnian interglacials, but during the Ipswichian interglacial, it expands and becomes important as soon as it appears in the record (West, 1970). Hazel (*Corylus*) is characteristically early in its immigration pattern (Fig. 2). It was never particularly successful until the last interglacial, when it expanded early in the interval. However, in the Holocene, it became dominant immediately in earliest postglacial time (Iversen, 1960); its brief success was caused by lack of competition, because hazel, a small tree, is easily shaded out of existence, or at least prevented from flowering, by the growth of forest trees. Rarity of hazel in previous interglacials may have been fortuitous, because in the order of arrival of immigrating trees, hazel always had competition from taller trees.

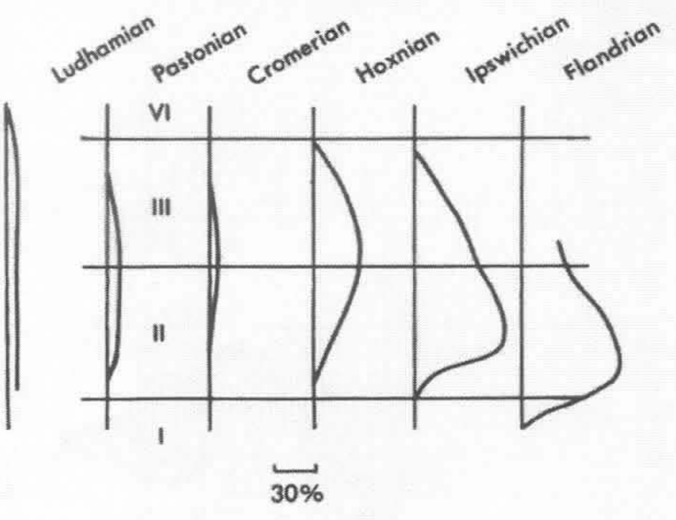

FIGURE 2. Hazel (*Corylus*) pollen percentages plotted against time for 5 interglacial intervals and the Holocene (=Flandrian) in East Anglia. Reprinted, with permission, from R. G. West, 1970. The pollen record indicates that the time of immigration and the relative abundance of this genus has varied widely from one interglacial interval to another.

All interglacials are similar in that they show a gradual increase in diversity as forest trees migrated into northern Europe. A pollen diagram from the last (Eemian) interglacial in Poland (Dabrowski, 1971) shows the increase in species numbers in a striking manner (Fig. 3).

Differences in the relative abundances of species in the deciduous forest communities of Europe during successive interglacials suggest that the same constellation of species formed alternate communities. The particular configuration of abundances in particular interglacial intervals may have depended largely on which species happened to arrive first. A similar mechanism is postulated for islands, where the first species to establish themselves and become abundant provide formidable competition for small populations of new immigrants (MacArthur, 1972). Another idea is that evolutionary development between interglacial intervals, which are, after all, about 100,000 years separated in time, has changed the competitive relationships among the tree species, causing differences in abundance in successive interglacials. The two ideas are not mutually exclusive.

Soils developed continuously during interglacial intervals. The sequences of sediments in lakes and the sequences of changes in the aquatic plant floras show progressive changes in water chemistry from basic to neutral to acid, indicating that groundwater and runoff changed as basic substances were leached from the soil. A similar sequence of development is documented for two interglacials in Denmark; in both cases, pollen in the upper fourth of the sediment profile records changes in terrestrial vegetation—expansion of heaths and other acidophilous plants—that document the changes in soil implied by water plants and lake sediment chemistry (Andersen, 1964). Soil development appears progressive over long time intervals. Rather than attaining equilibrium, with nutrient losses balanced by nutrient input, ecosystems undergo progressive, unidirectional changes. In some cases, they may become less productive as nutrients are permanently lost from the system. The changes in soil act as a forcing function for changes in vegetation, termed "retrogressive succession" by Iversen (1964).

INTERGLACIAL VEGETATION CYCLES: NORTH AMERICA

The variety of climatic provinces in North America and the virtual absence of cultural disturbance, make this continent an area of particular interest for the study of vegetation changes during interglacials. Unfortunately, interglacial floras are still inadequately known. Preliminary studies seem to show the same result as for Europe: communities contained a different spectrum of genera, or the same genera in different abundances in successive interglacials (Kapp and Gooding, 1964; E. Grüger, 1972a, b; Watts, 1969). However, the Holocene is known in detail; by anal-

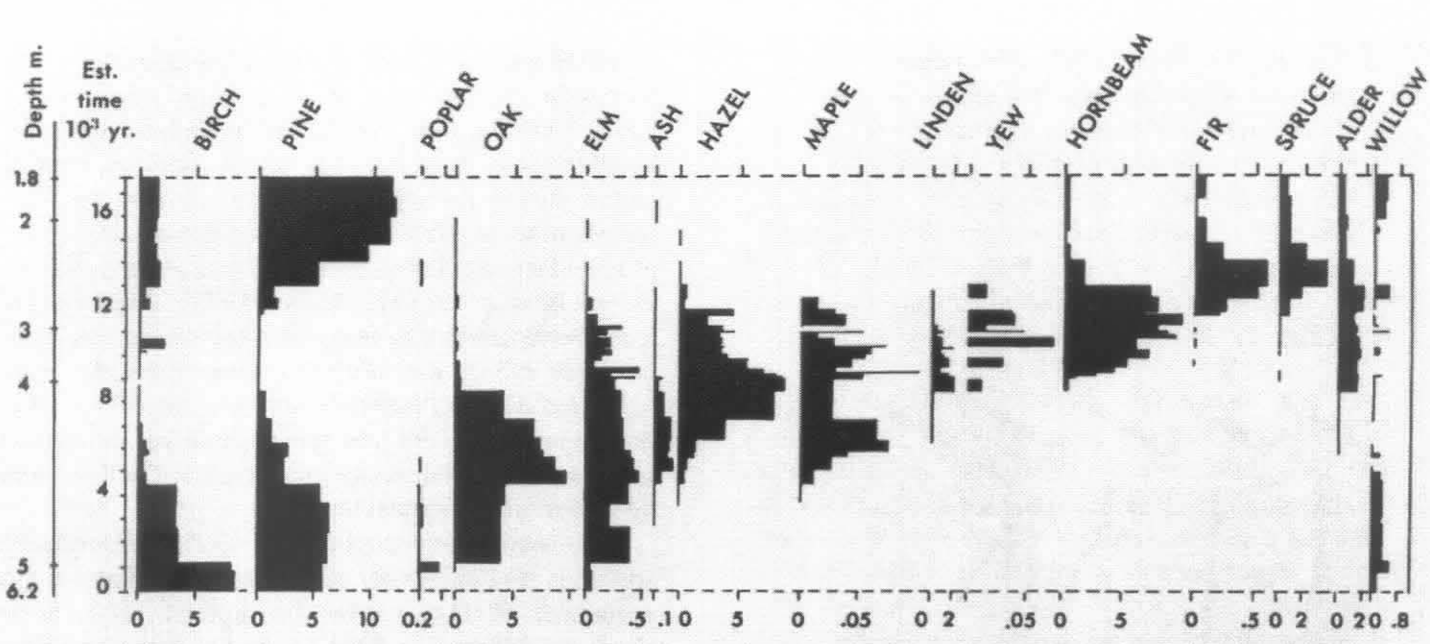

FIGURE 3. Absolute pollen frequency per cc of sediment in Eemian sediments from the last interglacial in Poland (redrawn from Dabrowski, 1971). The successive appearances of new genera throughout the interglacial is similar to the successive immigrations documented in American Holocene deposits.

ogy it can yield information about all previous interglacials. The Holocene began 10,000 years ago, when temperatures reached modern levels (in many regions). A temperature maximum, warmer than today, occurred between 5000 and 8000 years ago (Wright, 1972). The climate has been growing colder and more moist in the last few millenia, and montane glaciers have grown larger than at any time since the end of the last glaciation (Porter, 1967). By analogy with previous interglacials, which show a single temperature maximum, and by analogy with the time span of previous interglacials, the Holocene is now near its end and should be expected to terminate, with climatic changes that will destroy the deciduous forest, sometime within the next few centuries or millenia (Kukla *et al.*, 1972).

Biogeographers since Asa Gray have remarked on the diversity of deciduous forest in North America compared to Europe. They suggested that fewer extinctions occurred here than in Europe during the Pleistocene, because there were north-south-trending mountain chains, providing migration routes for flora escaping southward in response to climatic changes during glaciations. Braun (1950) suggested that the southern Appalachians were an area of stable climate, serving as a refuge during the Ice Age and as a source of species for recolonization of areas denuded of vegetation by the advancing ice sheet.

The newer palaeoecologic results show virtual elimination of deciduous forest, ruling out the southern Appalachians as a source area, and certainly climatic or floristic stability cannot be considered characteristic for the region. However, the idea of the Appalachian mountains as a migration route can be tested. A number of fossil sites exist where pollen evidence more or less clearly documents the first arrival of tree species. These sites have been summarized and maps prepared that show the migration sequence for several important forest species. Six such maps will be discussed in this paper. The maps are crude because they are based on few data, but they are important because they show the different source areas and directions of movement for different species, and for demonstrating that the rate of advance varied for each species.

Preparation of Migration Maps

Pollen sites used in the analysis are shown on the index map (Fig. 4)., but not all sites were used for each map. Small numbers on the migration maps indicate the estimated arrival times (in 10^3 yrs. P.P.) at particular localities. The localities used were chosen because there appeared to be good radiocarbon control (or reasonable correlation with sites having good radiocarbon control). The most subjective part of the

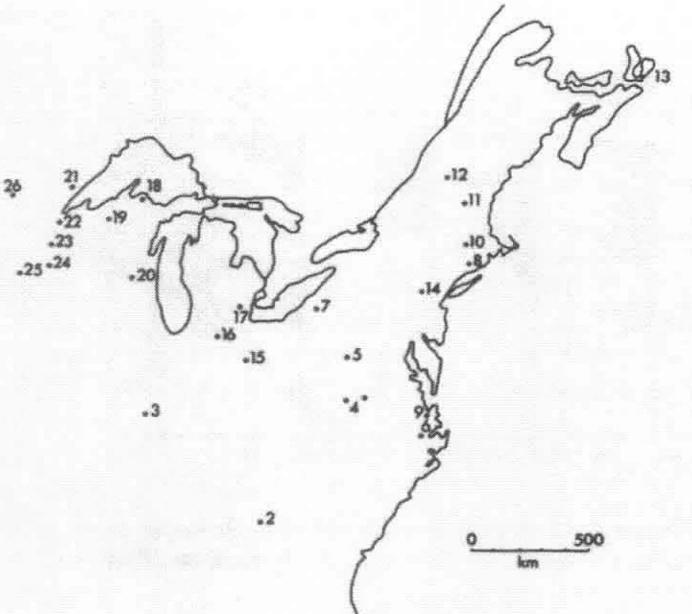

FIGURE 4. Outline map of eastern North America, showing sites used in the preparation of migration maps: 1, Watts, 1969; 2, Watts, 1970; 3, Grüger, 1972b; 4, Craig, 1969; 5, Maxwell and Davis, 1972; 6, Whitehead, 1973; 7, Walker and Hartman, 1960; 8, Davis, 1969; 9, Whitehead, 1972; 10, Davis, 1958; 11, Likens and Davis, 1974; 12, Davis, 1965; 13, Livingstone and Livingstone, 1958; 14, Niering, 1953; 15, Ogden, 1966; 16, Ogden, 1969; 17, Kerfoot, 1974; 18, Brubaker, 1973; 19, 20, Webb and Bryson, 1972, Webb, 1974; 21, Fries, 1962; 22, Wright, 1968; 23, Cushing, 1967; 24, Wright *et al.*, 1963; 25, Jelgersma, 1962; 26, McAndrews, 1966.

analysis was deciding the level of pollen influx that could be accepted as evidence for the arrival of a tree. Pollen percentages, more difficult to evaluate because of their dependence on the abundance of other species, were used only rarely, and then only where they could be correlated with nearby sites where absolute influx had been determined. I relied heavily on comparisons of modern influx and species boundaries in Michigan (Davis *et al.*, 1973). For example, hickory pollen influx is zero in the Upper Peninsula of Michigan far beyond the range of hickory, 100 grains cm^{-2} yr^{-1} in the northern Lower Peninsula, near hickory forests, and 800 grains cm^{-2} yr^{-1} in the oak-hickory region of the Lower Peninsula, where hickory now occurs with basal area of 0.25 m^2 ha.$^{-1}$. These levels correlate well with the fossil record at Rogers Lake, where low influx, not significantly different from zero, occurred until a few hundred years before a steep rise to 1000 grains cm^{-2}/yr, marking the arrival and sudden dominance of hickory in Connecticut forests (Fig. 5). A similar parallel can be drawn for pine, which has modern influx values of several hundred grains in southern Michigan, where pine is essentially absent. Influx values are only half as high during the early Late-glacial in Connecticut, indicating that pine was absent from the vegetation. The rise of jack/red pine influx to 2000 grains yr^{-1} 11,000 years ago indicates the arrival of one or both of these species, while the steep rise of white pine pollen 9000 years ago indicates the arrival of white pine (Fig. 5). Once decisions had been made relative to the interpretation of individual pollen diagrams, the dates of arrival were indicated on maps, and lines were drawn to show the positions of the migrating frontier at 1000-year intervals in the past. Additional subjectivity went into drawing these lines, which give a visual impression extending the density of the data points. There is no question that the migration lines will be modified in detail as additional data come to light, or even as different authors consider the same data, for example, J. C. Bernabo and Thompson Webb III (pers. comm.). I present them here because I believe that the general trends they show are probably correct.

Migrations of Dominant Forest Trees

Spruce (*Picea*) grew throughout the Midwest south of the ice sheet at the height of the last glaciation, 20,000 years ago. In the East it grew at low elevations (1500 ft. ?) on the slopes of the Appalachians and mixed with pine at the 1000-foot elevation in the Shenandoah Valley of Virginia. Spruce moved northward everywhere as the ice retreated, following the ice sheet northward in Minnesota (Wright, 1968). Larch (*Larix*) (Watts, 1967) and fir (*Abies*) (Grüger, J., 1973) were components of the spruce forest. In southern New England, spruce lagged behind glacial retreat; tundra grew in Connecticut for several thousand years after the ice had melted. The first forests to become established 11,500 years ago were open spruce woodlands. After a thousand years, spruce grew more densely, and alder (*Alnus*), fir, and jack pine (*Pinus banksiana*) grew together with spruce or separated from it on favored sites (Davis, 1967). Pollen evidence for northward movement of spruce as the ice border retreated farther north has

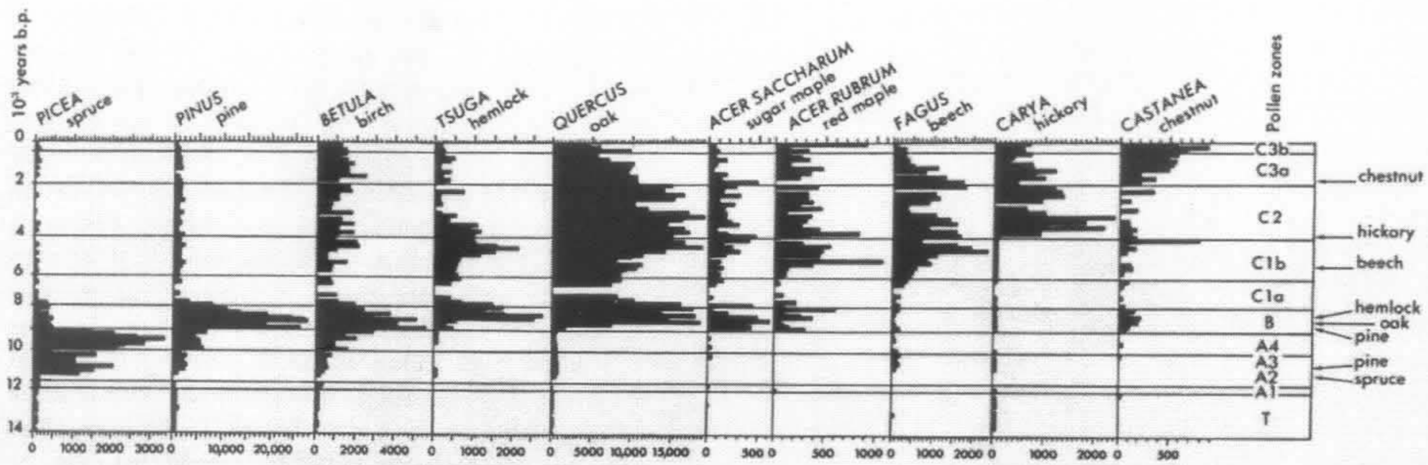

FIGURE 5. Pollen influx (numbers accumulated cm^{-2} yr^{-1}) at Rogers Lake during late glacial and Holocene time. Estimated time of immigration to Connecticut for a number of species is indicated to the right of the diagram. Time scale is to the left (modified from Davis *et al.*, 1973).

been summarized by Moran (1973) and by J. C. Bernabo and Thompson Webb III (pers. comm.). Wright also discusses the southern retreating edge of the Late-glacial spruce forest in his classic study of spruce and pine migrations (Wright, 1968).

Jack pine is the most conspicuous migrant following spruce. This tree became extinct in the central plains just prior to the glacial maximum, but it grew in abundance in the southeastern United States. The distribution was very different from today: jack pine is not especially abundant in eastern Canada, but it grows prolifically in the boreal forest of central Canada and in the mixed forests of the Great Lakes region. Migration to the central United States and thence to central Canada took place from the southeast; pine moved at a rate equivalent to 350 to 500 m per year for several thousand years (Fig. 6). Western movement stopped as pine reached a climatic region in which prairie had already replaced the spruce forest (Wright, 1968). Farther north, jack pine grew (briefly) in areas that were later invaded by prairie (McAndrews, 1966). While jack pine was limited by drought in the western part of its range, it continued for several thousand years to move northward into Canada to the region where it persists today. Outlying populations now occur in northern New England, apparent relics of its migration through the region in the early Holocene.

About 1000 years after jack pine, white pine (*Pinus strobus*) moved northward and westward (Fig. 7). It appears first at sites on the mid-Atlantic coast, but it is absent from sites farther south. This implies that white pine may have grown at least part of the time

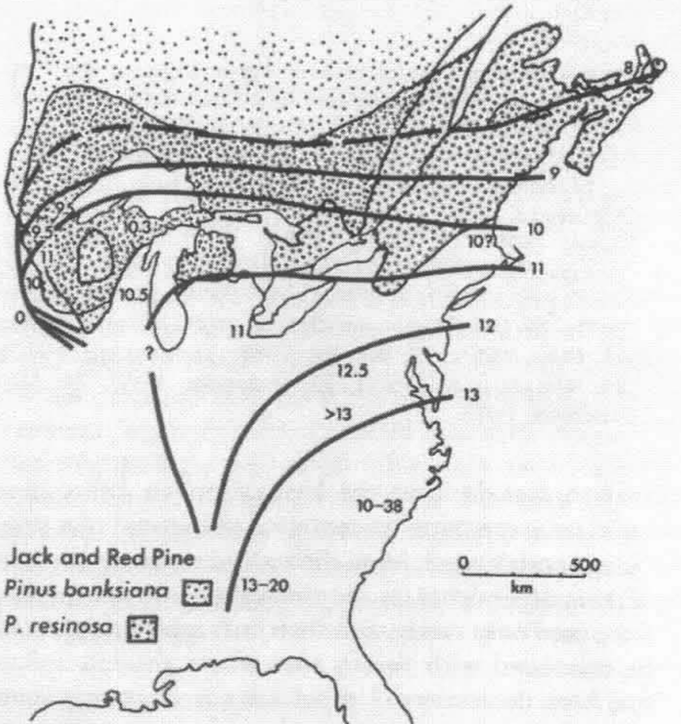

FIGURE 6. Migration of jack and/or red pine during the late glacial and early Holocene. Small numbers on the map indicate times of arrival at individual sites. Contours show the approximate location of the advancing frontier for the species at 1000-year intervals. Stippled area indicates modern range for jack pine; open circles indicate modern range for red pine.

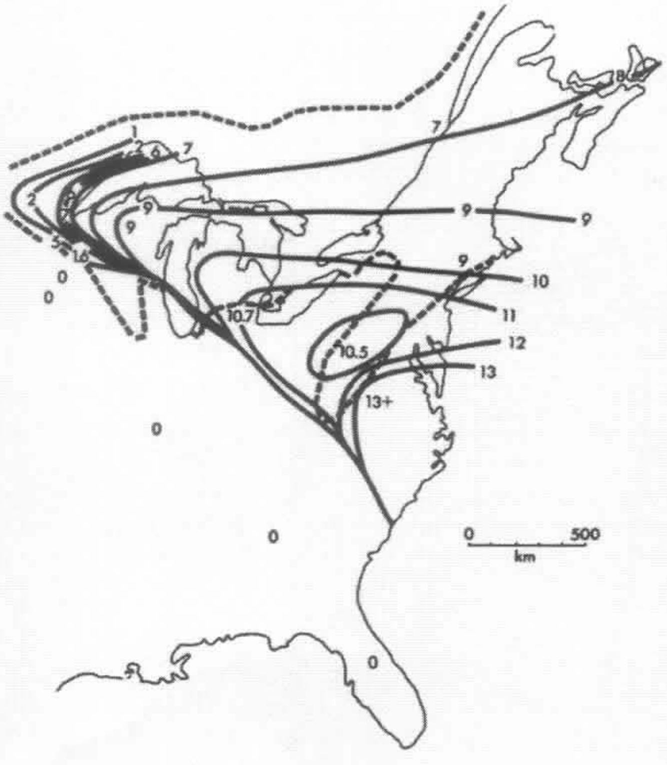

FIGURE 7. Migration of white pine. Small numbers on the map indicate times of arrival at individual sites; contours show the advancing frontier at 1000-year intervals. Dashed line surrounds the modern range for the species.

on the exposed continental shelf, long ago proposed as a possible migration route (Fernald, 1929; Deevey, 1949).

White pine also appears to have moved into Minnesota via a route north of the Great Lakes, as proposed by Wright (1968), reaching the western edge of Lake Superior at the height of the Prairie Period (5000–8000 years B.P.), when warm and dry climate prevented further westward movement. These same warm climatic conditions also permitted movement of pine far northward; macrofossils and pollen indicate that it grew in abundance north of its present limit 5000 years ago (Terasmae and Andersen, 1970). Subsequently the northern limit has contracted in response to climatic cooling, and population in New England and southern Canada has declined. Meanwhile the westward portion of its range has begun to expand, and white pine continues to move westward at the present time (Wright, 1968).

Oak (*Quercus*) increased in abundance at the same time white pine moved into deglaciated territory. I have not shown oak migration on a map because of difficulties in deciding which influx level indicates the actual presence of oak. However, oak is of particular interest in demonstrating that a heavy-seeded plant can be among the most rapid migrants.

Hemlock (*Tsuga canadensis*), a slow-growing, shade-tolerant species, was also one of the first to move northward, at the amazing migration rate of 200 to 300 m per year (Fig. 8). Its arrival at most sites is 500 to 1000 years later than white pine; apparently it was penetrating closed forests of pine, oak, birch, and maple. Hemlock reached maximum abundance in the northeast 5000 years ago, declining in frequency in more recent years. Its westward movement in Michigan was slowed by the hemlock population crash that occurred 5000 years ago (Davis, unpubl. data). At this time, hemlock had reached a point about halfway across the Upper Peninsula of Michigan. The population had recovered by about 4000 years ago, and it continued to move westward and southward. Presumably, hemlock is moving now in response to the more moist climatic conditions of the last few thousand years. Both hemlock and white pine are examples of species that are contracting along one boundary and expanding along another in

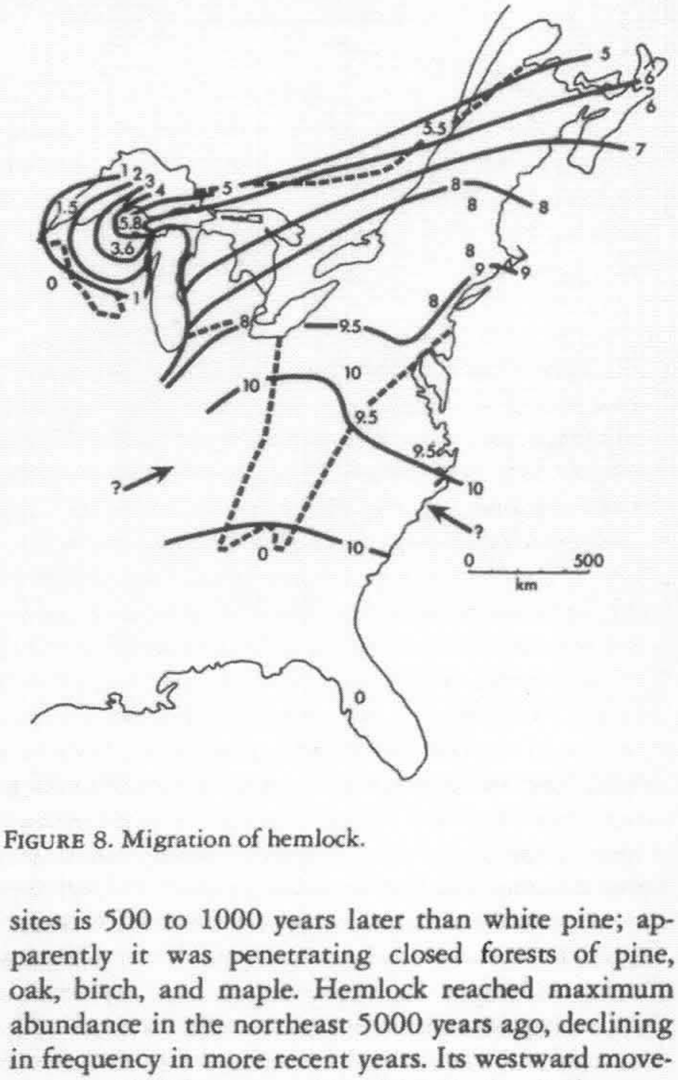

FIGURE 8. Migration of hemlock.

response to different expressions of the same climatic trend.

Beech (*Fagus grandifolia*) (Fig. 9) seems to have moved northward in the classic manner, moving north parallel to the Appalachian mountain chain at a rate of 250 to 300 m per year. It penetrated closed forest communities throughout its migration history. As a shade-tolerant species, the tree is adapted to seed in under a closed canopy; it would have difficulty moving into open habitats with pioneer vegetation. Pollen diagrams from Michigan (Brubaker, 1973; Davis, unpubl. data) indicate that beech has never been west of its present boundary and that it is in fact moving westward now. More data are needed to establish whether the movement has been continuous throughout the late Holocene, or whether it is a response to climatic changes of the last few centuries.

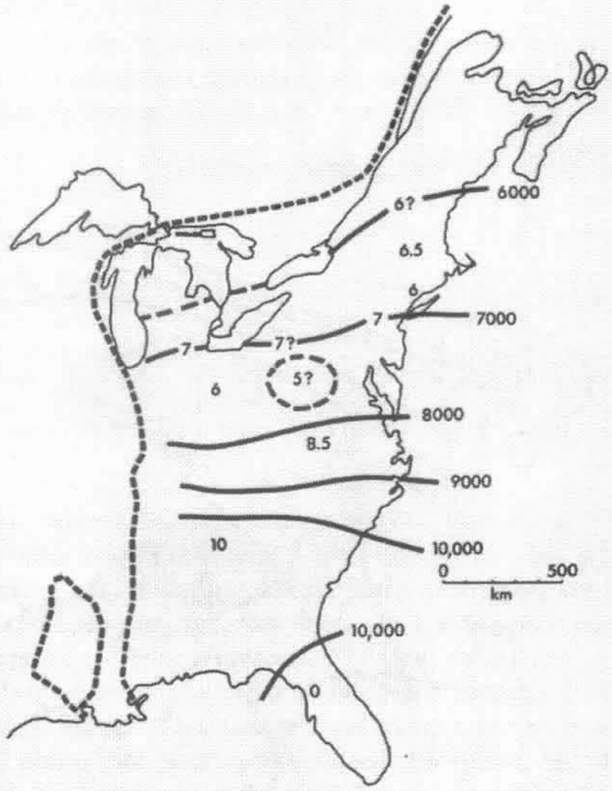

FIGURE 9. Migration of beech.

Hickory (*Carya*) appears first at sites in the West and South (Fig. 10), in accord with E. Grüger's assertion (1972a, b) that deciduous trees, especially species that grow along the prairie border, could have survived close to the ice margin in the southern Great Plains (Illinois). From the midcontinent, hickory moved eastward and northward. The migration rate has been relatively slow; hickory reached Connecticut only 5000 years ago, fully 5000 years after it had arrived in southern Michigan.

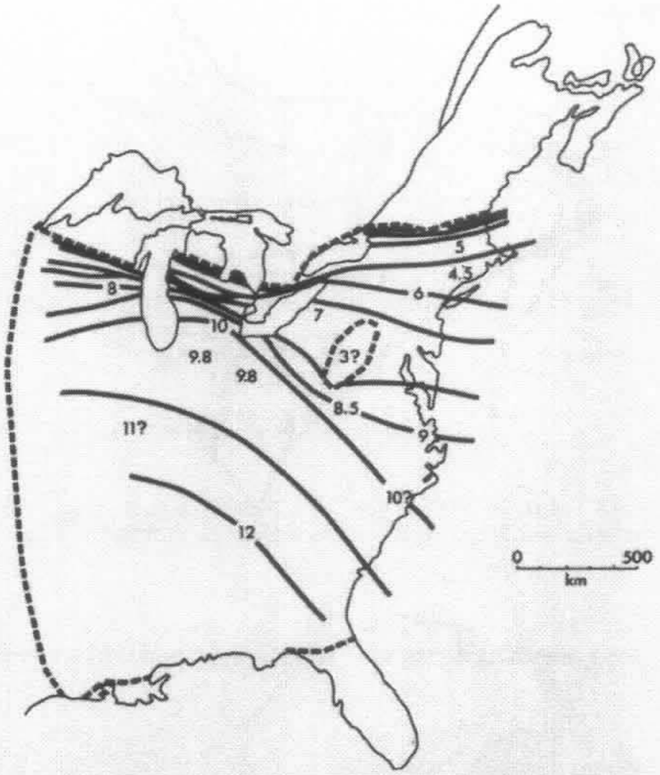

FIGURE 10. Migration of hickory.

Chestnut (*Castanea*) which moved from the East (Fig. 11), provides a contrasting history. Like white pine, it may have survived on the continental shelf, or at least it may have moved from its refuge, using the shelf as a migration route. It penetrated the deciduous forest slowly (100 m yr^{-1}), although it became a successful dominant species once it had arrived. It arrived in the Alleghenies 3000 years before it arrived in Connecticut. Both regions were mapped by Braun (1950) as oak-chestnut forest, yet this community in one region was 3000 years older than in the other.

DISCUSSION

Stratigraphy and Climatic Interpretation

Successive immigrations of trees cause a striking sequence of changes in pollen diagrams. For example, in Connecticut almost all the lower boundaries of pollen zones are defined by the arrival of migrating

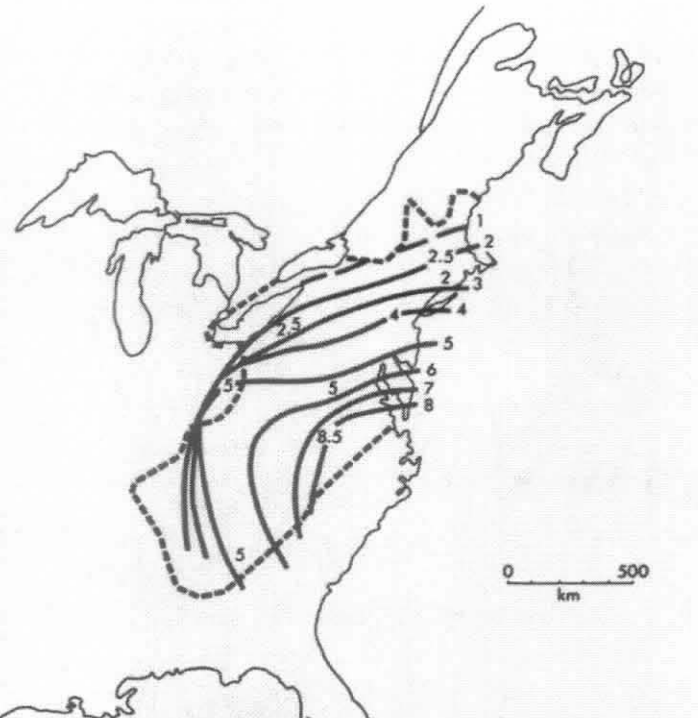

FIGURE 11. Migration of chestnut.

species: A (spruce), B (white pine), Clb (beech), C2 (hickory), C3a (chestnut) (Fig. 5). These pollen zone boundaries are only of local value, as they are time-transgressive whenever large regions are considered. Furthermore, the failure of hickory and chestnut to move far northward means that different criteria have to be used in northern New England to divide pollen diagrams into pollen zones. In northern New England, a drop in hemlock pollen abundance 5000 years ago, an event unrelated to, and not precisely synchronous to, the arrival of hickory in Connecticut, is used for the lower C-2 boundary. An increase in spruce pollen, the reflection of climatic cooling, is used to define C3a (Davis, 1965).

More serious is the problem of climatic interpretation. Clearly the sudden arrival of a species that is limited by migration speed cannot be attributed to climatic change, nor is its absence in older levels necessarily evidence for unfavorable conditions. But quite aside from the presence or absence of pollen, problems arise in interpreting abundances. The flora of the early Holocene was an impoverished flora, without modern analogues; it cannot be reconstructed through comparison with pollen assemblages in surface samples. The species list is different, as are the pollen percentages. Biotic factors are also important. Pine and oak, the earliest migrants, may have grown on many sites where they were later out-competed by new immigrants. Their ecological amplitudes might have been wider in the early Holocene than expressed at the present time. Under these conditions, one should be cautious in interpreting the environment by analogy with the present.

Ecology of Forest Communities

That forest trees are still migrating into deglaciated areas, even at the end of the Holocene interglacial interval, implies that the time span of an average interglacial is too short for the attainment of floristic equilibrium. Throughout the interglacial, species ranges will be adjusting to the new climatic regime, and biotic communities will continue to feel the impact of new invaders. During glacial intervals, which last longer, there are repeated oscillations in climate; all evidence points to similar floristic instability during glaciations, albeit involving somewhat different plant communities at different latitudes. Unstable conditions prevailed throughout the Quaternary, the period during which modern species evolved. It must be supposed that modern species are adapted to conditions of biotic instability.

The structure of deciduous forest communities has been subject to change throughout the lifetime of the particular communities we see before us, reducing possibilities for evolution of coadaptions among large species complexes. This generalization holds also for the species-rich, diverse deciduous forest communities of the southern Appalachians. Even those communities are a recent, chance conglomeration of species of trees that have immigrated into the area from different directions, from regions where populations existed just prior to the present (Holocene) interglacial.

The brief lifetime of the forest communities makes it unlikely that evolution could have produced homeostatic properties, including the ability to resist disturbing factors, such as invading species. The forests have been invaded repeatedly throughout the Holocene. It appears, then, that competition with invading species is relatively low, easing their entrance into the community.

Selection throughout the Pleistocene, rather than having produced stable communities, has apparently produced species that are successful in invading "closed" communities. Only successful invaders could have survived the interglacials, with the abrupt temperature rise that has terminated each glacial interval and introduced the interglacial climatic mode. A number of successful invading species, such as hemlock and American beech, are "climax" species, which become abundant following disturbance only after a prolonged, uninterrupted succession. As an example, in northern hardwoods forest, intervals as long as 600 to 700 years are necessary for beech and spruce to reach their equilibrium frequencies (Botkin *et al.*, 1972). These species can be classified only as "K-selected" species, adapted to compete as seedlings and saplings in stable "climax" communities. This adaptation is successful for invading such communities, for availability of seed appears less important than success in competing for space in the canopy. Other strategies are possible: for example, white pine, which requires sunlight, may invade by taking advantage of chance local disturbances, such as openings resulting from the blow-down of individual trees (Watts, 1973b). The mechanism of invasion of a forest community by new tree species is a matter of some interest to ecologists (Watts, 1973b; Andersen, 1973). Communities may be resistant to some species and easily penetrated by others. Such species as European beech and spruce, and some American deciduous trees and hemlock, have been successful immigrants, migrating rapidly and dominating forests soon after arrival. Others, such as the American chestnut, have migrated slowly, although they have become dominant once they arrived. Still others (European beech in previous interglacials is the only example that comes to mind) have been unsuccessful at moving or in becoming abundant. Presumably most such species have become extinct.

Acknowledgments

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